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Meulman, E J M ; van Schaik, C P

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E. J. M. Meulman
Anthropological Institute and Museum, University of Zurich

C. P. van Schaik
Anthropological Institute and Museum, University of Zurich

Introduction

Commonly referred to as a hallmark of human evolution, tool use is often considered a complex skill. Paradoxically, however, tool use seems to be widespread in the animal kingdom and may consist of fairly simple behavioral actions. In this chapter we try to relate these somewhat contradictory views to the relatively rare occurrence of habitual and complex tool use in wild orangutans, especially when compared to wild chimpanzees. We propose that, in addition to the previously suggested factors (i.e., extractive foraging, social tolerance and intelligence), terrestriality may have been instrumental in the evolution of especially habitual (*sensu* McGrew & Marchant, 1997) and complex tool use, thus explaining the "orangutan tool paradox." Our preliminary comparison of eight orangutan and ten chimpanzee study populations (descriptively, via a principal component analysis (PCA), and by testing predictions related to the four factors) does indeed point in this direction.

Defining tool use

Although tool use has been defined in various ways (see Shumaker *et al*., 2011 for a detailed discussion), we choose to follow the definition of Parker and Gibson (1977):

> Tool use is the manipulation of an object (the tool), not part of the actor's anatomical equipment and not attached to a substrate, to change the position, action, or condition of another object, either directly through the action of the tool on the object or of the object on the tool, or through action at a distance as in aimed throwing. (Modified from Parker & Gibson, 1977; Sanz & Morgan, 2007)

We did not adopt the new definition proposed by Shumaker *et al*. (2011) because we believe that the criterion that objects are "not attached to a substrate" is very important. This condition may be particularly relevant for the evolution of complex tool use, because detached objects can be more easily modified and can be incorporated more

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flexibly into tool combinations/sequences. We also avoided making inferences about an animal's intentions when using tools (e.g., to alter more efficiently the form, position or condition of another object, organism or the user itself: Beck, 1980). Therefore, Parker and Gibson's (1977) definition seems the most appropriate for this chapter.

Tool use as reflection of a cognitive gradient

The significance of tool use lies in what it reveals about the cognitive abilities of its users. Although cognitive abilities may be reflected in many tasks, tool use provides us with the clearest window into the cognitive abilities underlying animal behavior (Byrne, 1995). This is not because tool use requires advanced cognition *per se*, but rather because of the cognitive gradient that can be recognized when animals use objects. This ranges from the fairly simple manipulation of fixed substrates or borderline tool use to: *true* tool use in which objects are detached from their substrate (although use may still be stereotypic and inflexible); additional steps of manufacture and modification (Beck, 1980; Boesch & Boesch, 1990; McGrew, 1992; Bentley-Condit & Smith, 2010); flexible tool use, in which the tools are adjusted to the task at hand (van Schaik *et al*., 1996); and finally accumulated tool use (also: cumulative or associated) in which multiple innovations (cf. Reader & Laland, 2002) may be combined for a single purpose (Parker & Gibson, 1977; Beck, 1980; Byrne, 1995; Bentley-Condit & Smith, 2010; Shumaker *et al*., 2011). Flexible and cumulative tool use in particular reveal the operation of intentions or mental simulation and planning, rather than direct responses to stimuli (Byrne, 1995), and therefore can be considered intelligent (Parker & Gibson, 1977).

Defining "complex" tool use

For this chapter we focus especially on the complex end of the tool-use gradient because of our interest in "the orangutan tool paradox:" i.e., the rare occurrence of complex tool use in wild orangutans, although such complex tool use is fairly common for rehabilitant or captive orangutans (cf. van Schaik, 2004). Complex tool use has been defined in varying ways as well (Sanz & Morgan, 2010; Shumaker *et al*., 2011). Here we define complex tool use as tool use that includes more than one element (accumulated), because the number of constituent elements will generally be correlated with the difficulty of learning and because hominin technology is characterized by increasing accumulation (cf. Haidle, 2010; Pradhan *et al*., in press). Where known, accumulated techniques are also generally accompanied by flexibility (adjustment to the task at hand) and acquisition through social learning (any kind of learning that is triggered or influenced by other group members or conspecifics [cf. Fragaszy & Perry, 2003] and thus including also socially facilitated individual learning via, for example, stimulus enhancement). However, because these latter two aspects are less consistently reported in the literature, we focus on the accumulation criterion. This may not be perfect, in that some non-accumulated tool-use techniques may be cognitively challenging as well, but this is the most practical division of the complexity gradient.

Evolution of primate tool use

Apart from the insight it provides into cognitive abilities, tool use is also interesting from the perspective of human evolution. Among all tool-using taxa, primates are unique in the variation they show in tool-using contexts (Bentley-Condit & Smith, 2010). Nonetheless, habitual and complex tool use have often been considered a hallmark of hominins. Habitual tool use here refers to those tool-use variants that have been seen repeatedly in several individuals, consistent with some degree of social transmission (*sensu* McGrew & Marchant, 1997), excluding branch throwing in agonistic contexts, which is universal among primates. Within the primate order, only chimpanzees (McGrew, 2004b; Sanz & Morgan, 2007, 2009), orangutans (van Schaik *et al*., 1996), some capuchins (Ottoni & Izar, 2008; Visalberghi *et al*., 2009) and possibly some long-tailed macaques (Gumert *et al*., 2009) are known to be capable of habitual tool use in natural conditions.

To explain the evolution of tool use in primates, van Schaik *et al*. (1999) proposed a socioecological model that includes a nested series of conditions. Tool use will be performed in broader contexts only when the primates engage in extractive foraging and are capable of dexterous manipulation (first two conditions). Species with more advanced innovative ability (intelligence) can also manufacture tools in both captivity and the wild (third condition). Subsequently, social tolerance allows for the spread of tool innovations within a population, allowing for habitual tool use and material culture (fourth condition). Finally, the ability for teaching in humans further allows for cumulative culture (fifth condition).

The potential role of terrestriality

Although the socioecological model explains the broad distribution of aspects of primate tool use, it cannot explain the rarity of complex tool use in all wild orangutans (van Schaik *et al*., 1996) relative to chimpanzees (Whiten *et al*., 2009). We would therefore like to propose to add terrestriality as a factor to the model. A terrestriality effect on tool innovations (especially for extractive foraging) and complex manipulations has already been suggested in various previous studies (e.g., McGrew, 2004a; Visalberghi *et al*., 2005; Humle & Matsuzawa, 2009; Spagnoletti *et al*., 2009; but see Boesch-Achermann & Boesch, 1994). However, here we propose that terrestriality may not only affect opportunities for (complex) tool innovations, but may also affect opportunities for socially facilitated tool-affordance learning (*sensu* Huang & Charman, 2005), because previously used tools are more easily encountered in a terrestrial setting (see also Meulman *et al*., in press). Terrestriality may especially promote the occurrence and transmission of complex tool use, because accumulated technology is less likely to be invented independently and therefore relies more critically on propitious learning conditions. Orangutans are arboreal and appear to lack complex tool use. Thus, they provide us with an excellent opportunity to study the conditions favoring the origins of complex tool use, and hence the foundation of hominin cumulative technology.

Orangutans

Among the great apes, orangutans are the least related to humans. The current consensus among paleoanthropologists is that the orangutan lineage and that of the other great apes separated around 14 mya (Kelley, 2002; Raaum *et al*., 2005). Today, orangutans are only found on the islands of Sumatra and Borneo, in Southeast Asia. They are commonly subdivided into two species, the Sumatran *Pongo abelii*, and the Bornean *Pongo pygmaeus* (Xu & Arnason, 1996; Warren *et al*., 2001). The existing taxonomic subdivision of the three Bornean subspecies (*P. p. pygmaeus*, *P. p. wurmbii* and *P. p. morio*), described on the basis of morphological characteristics (Groves, 2001), however, does not adequately capture the genetic variation within this species (Arora *et al*., 2010).

Orangutans are large-bodied great apes that live in habitats varying from coastal peat swamp forest to montane dryland rainforest. They mainly differ from the African great apes in that females are almost exclusively arboreal, and, despite variation in gregariousness across populations, are generally semi-solitary. Bornean males are more terrestrial, but almost exclusively solitary apart from brief consortships with females (Utami-Atmoko *et al*., 2009).

Ecologically, orangutans are much like chimpanzees, being frugivorous and omnivorous foragers with a large dietary repertoire. This includes extractive foraging, which means that they extract food items from the matrices in which these items are embedded. Orangutans feed, for example, on seeds of *Polyalthia glauca* after first discarding the foul-tasting pulp, and remove the seeds of *Neesia* sp., without even touching the prickly matrix embedding them. Insects or their products (e.g., honey, larvae) are extracted from nests that are often located in tree holes, or picked up after pulling bole climbers off the trunk. Pith is extracted from hearts or stems of palm trees or the young twigs of *Dyera costulata*, and tree cambium is scraped off inner bark, after first removing the outer bark of tree trunks. Because all these items are embedded in a matrix that is hard, or even dangerous, animals must learn to identify them as food and overcome their defenses. This strong reliance on extractive foraging leads us to expect abundant tool use in orangutans.

This study

Updating the orangutan tool catalog

In this chapter we have compiled all available information on wild orangutan tool use to create an updated overview of the orangutan tool repertoire and to compare this to the chimpanzee tool repertoire. To allow for fair comparison, and to exclude effects such as enculturation that are less directly relevant for understanding the occurrence and evolution of tool use in primates, only wild populations were considered.

Describing the variation in tool repertoires

To establish the main components distinguishing tool repertoires across sites, and to gain insight into the level of interdependency between outcome variables, one can conduct a

PCA. Eight outcome variables (or nine when we included nest variables – see discussion) were included as a potential source of variation in the tool repertoires. These included three context-related variables to help us to better discriminate between different aspects of the tool repertoire and innovation biases that may exist. Based on the socioecological model of van Schaik *et al*. (1999) we expect the following outcome variables to cluster together: (1) intelligence – physical-comfort tool variants (non-extractive), total number of tool variants, complex tool variants; (2) extractive foraging – extractive foraging tool variants, subsistence tool variants, total number of tool variants; (3) social tolerance – cultural tool variants, communication tool variants, total number of tool variants. However, if we include the potential terrestriality effect, we expect terrestrial, extractive, cultural, complex, subsistence, communication and the total number of tool variants to cluster together because of the potential positive effect of terrestriality on extractive foraging, social learning and the acquisition of complex skills. The second component should then include physical comfort tool variants and the total number of tool variants.

Predictions of the new model

To gain some insight into the independent effects of each of the four predictor variables on the variation in tool repertoires across sites and the importance of interactions between predictor variables, a multiple regression analysis would have been ideal. Sample size, however, did not allow for a multiple regression analysis to predict the best explanatory model for each component extracted from the PCA. We decided to use bivariate analysis as an alternative method for testing the predictions regarding the effects of the four factors on the tool repertoires of the various orangutan and chimpanzee populations. Although these analyses ignore possible interaction effects among the factors, we believe they do help us understand the extent of the direct effects of the four factors on the tool repertoire. Hence, although preliminary, these results should give us an idea of the best explanatory model for the variation in tool repertoires.

We will now discuss the proxies used for each factor and develop predictions for the expected differences among orangutan populations and between orangutans and chimpanzees.

Testing the role of intelligence

Intelligence can be viewed as general cognitive ability (Deaner *et al*., 2007; Reader *et al*., 2011). Although the best proxy measure of such general cognitive abilities or intelligence is still highly debated, these studies showed that absolute measures of brain provided a far better fit than body-size-corrected measures such as the encephalization quotient. We therefore considered absolute correlates of cranial capacity to be a valid proxy for intelligence, especially given that female great apes are quite similar in body size. An additional advantage of taking this measure is that it allows us to compare the different orangutan species and subspecies.

For females, cranial capacity is almost identical between chimpanzees and orangutans (Isler *et al*., 2008). Among orangutans, however, *P. p. morio* (northeast Borneo) have significantly smaller cranial capacities than the Sumatran orangutans (*P. abelii*),

Table 9.1 Predictions depending on the potential terrestriality-effect. Predicted differences in tool repertoire between orangutan populations and between orangutans and chimpanzees.

Role of. . .	Measure	Kind of tools	OU-B vs. S	OU vs. CH (−terrestriality)	OU vs. CH (+terrestriality)
Intelligence	Cranial capacity	Non-extractive	B (*m*) < B, S (n*m*)	OU(n*m*) = CH	OU(n*m*) ≤ CH
		Complex	B (*m*) < B, S (n*m*)	OU(n*m*) = CH	OU(n*m*) < CH
Extraction	Insectivory	Extractive	B (n*m*) < S	OU(n*m*) = CH	OU(n*m*) < CH
Opportunities for social learning	Social tolerance	Cultural	B (n*m*) < S	OU(n*m*) < CH	OU(n*m*) << CH

Notes
B = Bornean orangutans; S = Sumatran orangutans; m = *morio*; n*m* = non-*morio*, OU(n*m*) = non-*morio* orangutans; CH = chimpanzees; −/+terrestriality: ex-/including potential terrestriality effect, respectively. For orangutans the exclusion or inclusion of the potential terrestriality effect has no effect on the predictions. The first three columns describe what has been tested, the last three columns describe the predictions for each comparison and test.

with *P. p. wurmbii* (central Kalimantan/southern Borneo) being intermediate but closer to *P. abelii* (Taylor & van Schaik, 2007). We therefore considered *P. p. morio* somewhat less intelligent than the other orangutan subspecies (although this has not been formally tested). Nevertheless, we also report the results when *P. p. morio* were included in the analyses. We expected no differences between chimpanzees and (non-*morio*) orangutans in general (see also Deaner *et al*., 2007; Reader *et al*., in press.).

The prediction is that innovative ability, as proxied by intelligence, predicts total tool repertoire size (see also Reader & Laland, 2002). However, the latter may be confounded by other variables. First, given the known variation in reliance on extractive foraging, a cleaner estimate of the role of intelligence would be to examine the repertoire size of tool variants *not* used for extractive foraging. Second, variation among populations and species in opportunities for social learning may affect the likelihood that innovations persist. Thus, it is possible that the total repertoire is greater in species or populations with better opportunities for social learning (van Schaik, 2006). Hence, tool complexity may be a better measure of intelligence, although it in turn may be affected by terrestriality and opportunities for social learning (see below). We will therefore use the total repertoire of non-extractive tool variants and tool complexity as preliminary estimates of the effect of intelligence (Table 9.1).

Testing the role of extractive foraging

Currently few quantitative estimates for extractive foraging frequency exist. The effect of extractive foraging opportunities is best estimated by comparing the total repertoire of extractive tool variants. As almost all insectivory is extractive, insectivory may be the best proxy for estimating tendencies toward extractive foraging (van Schaik *et al*., 1999). This is especially likely since other extractive activities are not amenable to support by tool use (e.g., the extraction of cambium or bark by Bornean orangutans). Nevertheless, to validate this, we need to establish that most insect foraging is indeed extractive. Data confirm this (Tuanan: >95%, M. A. van Noordwijk, 2010, unpublished data; Suaq

Balimbing: >75%, Sitompul, 1995). Overall, Sumatran orangutans are more insectivorous than Bornean orangutans (11% of the total feeding time in Sumatran populations, about 5.7% for *P. p. wurmbii*, and ca. 1.4% for *P. p. morio*) (Morrogh-Bernard *et al*., 2009). It is commonly thought that chimpanzees rely more on extractive foraging than orangutans. However, the mean percentage of insectivory across chimpanzee populations is around 4% (Stumpf, 2007), similar to Bornean orangutans. Thus, until future work provides better estimates of the incidence of extractive foraging, it is parsimonious to expect that Sumatran orangutans have more extractive foraging tool variants than Bornean orangutans, but that there are no systematic species differences between the two great ape species (see Table 9.1).

Testing the role of social tolerance

Opportunities for social learning will depend on the degree of tolerant proximity (Coussi-Korbel & Fragaszy, 1995). Among orangutans, Sumatran populations are much more gregarious than the Bornean populations (van Schaik, 1999; van Noordwijk *et al*., 2009), largely due to differences in forest productivity and food availability (van Schaik, 1999; Marshall *et al*., 2009). Most chimpanzee populations are more gregarious than orangutans (van Schaik *et al*., 2003c). Thus, chimpanzees have more opportunities for social learning than orangutans, and Sumatran orangutans have more than Bornean orangutans. The size of the cultural-tool repertoire is usually considered to be a good estimate for the effect of opportunities for social learning (see Table 9.1).

Testing the role of terrestriality

The increased innovation tendencies are expected to primarily affect the number of (terrestrial) extractive tool variants. Moreover, as explained above, enhanced social learning opportunities should increase the number of complex tool variants within the repertoire more than the simple forms. We therefore predict that the socially tolerant terrestrial chimpanzees have more extractive (cultural) and complex (cultural) tool variants in their repertoire than the (socially tolerant) non-terrestrial orangutans. This contrasts with the predictions of the socioecological model (see Table 9.1). Moreover, we expect that tools used on the ground are more complex than tool variants used in arboreal settings. Because orangutans are rarely terrestrial and usually solitary (aside from consortships), we expect no differences in tool complexity between the various orangutan populations due to terrestriality (Table 9.1).

Methods

Orangutan tool catalog

Despite the recent wave of interest in innovation and culture in orangutans, so far no complete tool catalogs have been compiled for wild orangutans (but see Fox & Bin'Muhammad, 2002). We therefore reviewed the literature on tool use, innovations and culture in wild orangutans (Russon *et al*., 2009; van Schaik *et al*., 2009), and added

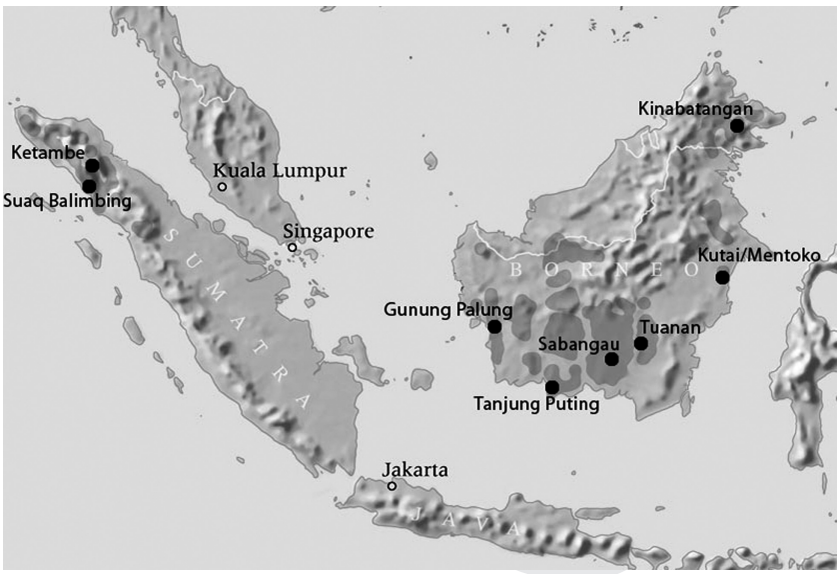

Figure 9.1 Map showing the locations of the eight orangutan study sites that have been included in the tool catalog. Dark-shaded areas indicate orangutan distribution.

some unpublished observations from Suaq Balimbing, to construct a tool-use inventory for eight wild orangutan populations in Sumatra and Borneo (Figure 9.1). We trust that this provides us with the complete tool repertoire for orangutans at existing study sites (especially for the habitual tool variants), because tool-use behaviors are striking to observers and have been a focus of attention for at least three decades (van Schaik *et al*., 1996; Fox & Bin'Muhammad, 2002).

Chimpanzee tool catalog

For the species comparison to chimpanzees we used the chimpanzee tool repertoire as reported by Sanz and Morgan (2007). We additionally included one new tool variant reported for Goualougo – "ant nest perforation" (Sanz *et al*., 2010). For information about cultural status, tool complexity and terrestrial use, see Meulman *et al*. (in press).

Criteria for the inclusion of tool variants in the tool catalog

To be able to compare orangutan tool repertoires with those of chimpanzees, we applied the same criteria for the inclusion of tool variants as reported by Sanz and Morgan (2007) (see also Whiten *et al*., 2001). Hence, dependent on the similarity of the action patterns, tool variants were split or lumped. Similar criteria have been reported in the literature on cultural behavioral variants in wild orangutans (van Schaik *et al*., 2003a; Wich *et al*., 2009).

"Accidental" innovations reflect the potential for innovation and flexible and complex tool use, and have also been included in the chimpanzee tool catalog described by Sanz and Morgan (2007). We therefore included them here as well to facilitate unbiased

comparisons. For the same reason, we excluded objects for which accidental use or use in play could not be excluded, as well as nest elements, given that nest-building activities are generally not considered as tool use (Beck, 1980). We will nonetheless discuss nest-building elements, since we think that some involve true tool use (i.e., nest pillow, nest blanket, nest lining, nest roof, artistic pillow), and are important from a cognitive and evolutionary perspective (see discussion).

Classification of tool variants

The most basic measure for the variation in tool repertoire across sites is the total repertoire of tool variants for a given population. All tool variants in the tool catalog were subsequently evaluated in terms of their classification as extractive foraging, cultural, complex and terrestrial; and their context use in terms of subsistence, physical comfort or communication.

A subset of the total tool repertoire is the repertoire of tool variants used for extractive foraging: tool variants used to extract an edible item from an inedible matrix. Based on this definition, tools used to obtain water from tree holes (e.g., sponging) were considered extractive foraging tool variants, whereas tools used to obtain water from ponds or streams were not (e.g., algae scoop).

Another subset is the cultural tool repertoire of a population. We identified putative cultural tool variants as those behavioral patterns that are absent without ecological explanation in at least one community, yet achieve at least habitual status in at least one other community, excluding those that are species universals (i.e., at least habitual prevalence observed at each site and therefore thought to have more canalized development (Whiten *et al*., 1999). This approach has recently been validated for orangutans (Krützen *et al*., 2011).

A fourth measure is the complexity of the tool variants. We classified tool variants as complex when the accumulation of tools, including the particular tool variant (e.g., in tool sets or combined tool use *sensu* McGrew, 2010), has been reported in the literature.

Tool variants may be used exclusively in arboreal conditions or in terrestrial conditions as well (a fifth measure or outcome variable). They can furthermore be classified according to the context in which they were used (*sensu* van Schaik *et al*., 2006): subsistence, physical comfort and communication (outcome variables 6–8). In instances of doubt, tool variants were classified according to their direct purpose. Hence, tooth-cleaning tools, for example, were classified as physical comfort tool variants because they were not used to assist feeding but used after feeding to enhance physical comfort or hygiene. Where multiple contexts were possible, we chose the predominant one (e.g., a branch swatter is mainly used to protect against insects while resting, but can also assist in feeding on bees' nests).

Statistical analysis

Given the small sample sizes, we used (if possible) non-parametric statistical tests with exact *p*-values two-tailed), and also reported trends. The repertoires of the three

orangutan subspecies were compared with the Kruskal–Wallis test. Mann–Whitney U tests were used to compare orangutan with chimpanzee repertoires. The distribution of tool variants over the three behavioral contexts was tested with a Chi-square over the 81 tool variants (chimpanzees: $n = 43$, orangutans: $n = 38$).

We conducted a PCA with orthogonal rotation (varimax) to extract the factors relevant for distinguishing tool repertoires of different study sites, and to look at the clustering of the various subsets of tool variants. Bivariate correlation analyses were conducted to test the effect of study duration on the eight outcome variables included in the PCA.

To test the effect of the four factors proposed to be relevant for the evolution of tool use, populations and (sub)species were compared with the Mann–Whitney U test by taking the mean number of tool variants per long-term study site, to control for sampling intensity (chimpanzees: $n = 10$; *P. p. wurmbii*: $n = 4$; *P. p. morio*: $n = 2$; and *P. abelii*: $n = 2$ study sites). Furthermore, we performed Mann–Whitney U tests to evaluate whether complex tool variants differed from simple tool variants recorded for orangutans and chimpanzees (total $n = 81$) in being used more terrestrially and/or extractively.

Results

Tool catalogs

For wild orangutans a total of 38 (true) tool variants (excluding five nest-building variants that could also be considered true tool use) have been reported (see Table 9.2). This number includes a hitherto unpublished variant, the "straw tool": using a tool to drink water from a tree hole or hole in the liana bark ($n = 3$ observations). The entire catalog included seven tool variants used for extractive foraging (amounting to 18% of the total repertoire); 16 tool variants that were potentially cultural (42%); two (5%) were used in terrestrial contexts; and zero variants contained multiple elements and hence were considered complex. All five nest elements (not included in the above-mentioned totals) were classified as non-cultural, complex, physical-comfort tool variants. Regarding the context, 13 (34%) of the orangutan tool variants were used in the subsistence context, 18 (47%) for physical comfort and seven (18%) for communication.

Figure 9.2 shows the distribution of tool variants over the eight wild orangutan study sites included in the analysis. The figure indicates that differences regarding the number of tool variants between the subspecies are all in favor of *P. abelii*, against *P. p. morio*, with *P. p. wurmbii* being intermediate. Only the total number of tools differed significantly among the three subspecies ($\chi^2(2) = 6.1$; $p = 0.014$), whereas a trend was observed for the number of extractive tool variants: $\chi^2(2) = 5.1$; $p = 0.057$. The number of complex, cultural, subsistence, physical-comfort and communication tools did not differ significantly among the subspecies. A bivariate correlation analysis revealed no significant correlation of study duration with any of the eight outcome variables.

The chimpanzee catalog included 43 variants, including 23 (53%) extractive, 17 (40%) complex, 23 (53%) cultural and 32 (74%) terrestrial tool variants. With regard to the context, 26 (60%) of the chimpanzee tool variants were used for subsistence, 12 (28%) for physical comfort and five (12%) for communication. Sanz and Morgan (2007) also

Table 9.2 Orangutan tool catalogue. An overview of all the tool variants (including nest elements) reported for wild orangutans; comparing their presence across eight long-term orangutan study populations.

	Study sites												
Tool variant	Cont.	EF	Cult.	GP	TP	SA	TU	KU	KI	KE	SB	Ref	Source
Leaf bundle ("doll")	2	0	0	R	R	A	R	A	A	R	A	1	T 21.2, 20.1
Auto-erotic tool	2	0	1	A	A	A	A	P	A	C	A	1	T 21.1, 20.1
Bee cover	2	0	0	A	A	A	R	A	P	P	R	1–3	T 21.2, 20.1
Branch cushion	2	0	1	R	H	H	C	?	A	H	C	1,3	T 21.1, 20.1
Branch hide	3	0	0	A	R	A	A	P	R	R	R	1–3	T 21.2, 20.1
Branch hook	2	0	0	A	A	R	R	?	A	?	R	1,3	T 21.2, 20.1
Branch reach fruit	1	0	0	A	R	A	A	A	A	A	A	2	
Branch scoop	1	1	1	A	A	H	A	A	A	A	H	1	T 21.1, 20.1
Branch as swatter	1	0	1	R	R	R	A	H	H	H	H	1	T 21.1, 20.1
Branch fan	2	0	0	?	?	?	?	?	?	?	?	2	
Branch dragging display	3	0	0	A	A	A	A	?	R	E	E	1	T 21.2, 20.1
Foam leaf body	2	0	1	A	A	H	A	?	A	A	A	1	T 21.1, 20.1
Club	3	0	0	R	A	A	A	A	A	A	A	2	
Leaf wipe	3	0	1	A	C	A	A	A	A	A	R	1,3	T 21.1, 20.1
Kiss-squeak leaves	3	0	1	C	A	R	H	H	A	R	R	1,3	T 21.1, 20.1
Leaf cushion	2	0	1	E	R	E	E	A	R	C	A	1,3	T 21.1, 20.1
Leaf glove (bite)	1	0	0	A	A	R	A	?	?	R	A	1,2	T 21.2, 20.1
Leaf glove (spine)	1	0	1	E	R	E	E	A	R	H	A	1,3	T 21.1, 20.1
Leaf napkin	2	0	1	A	A	A	A	C	A	R	R	1,3	T 21.1, 20.1
Poultice use	2	0	0	A	A	R	A	?	A	A	A	1	T 21.2, 20.1
Leaf scoop	1	0	0	R	A	A	A	A	A	A	A	1	T 21.2, 20.1
Sponging	1	1	0	A	A	R	A	A	A	R	A	1	T 21.2, 20.1
Moss cleaning	2	0	1	A	A	H	A	?	A	A	A	1	T 21.1, 20.1
Leaf wiper	2	0	0	R	A	R	A	A	A	A	A	1	T 21.2, 20.1
Aimed missile	3	0	0	C	C	C	C	C	C	C	C	2	
Nail cleaning	2	0	0	?	A	A	A	?	?	P	A	1	T 21.2, 20.1
Hat cover	2	0	0	C	C	C	C	C	C	C	C	1,2	T 21.2
Scratch with stick	2	0	1	A	R	R	R	H	A	A	A	1	T 21.1, 20.1
Snag crash	3	0	0	C	C	C	C	C	C	C	C	1	P 21.3.3

Snag riding	2	0	1	A	C	R	H	A	A	A	R	1,3	T 21.1, 20.1
Stick as chisel (1-Nest)	1	1	0	A	R	A	A	A	A	R	A	1	T 21.2, 20.1
Stick as chisel (2-Durian)	1	1	0	A	A	A	E	A	A	R	A	1	T 21.2, 20.1
Stick push spine	1	0	0	A	A	A	E	?	A	R	A	2	
Seed-extraction tool use	1	1	1	A	A	E	E	E	A	E	C	1	T 21.1, 20.1
Tree-hole tool use	1	1	1	A	A	A	A	A	A	A	C	1	T 21.1, 20.1
Straw tool	1	1	0	A	A	A	A	A	A	A	R	2,3	
Tooth cleaning (leaf)	2	0	1	H	A	A	H	?	C	A	A	1	T 21.1, 20.1
Tooth pick (stick)	2	0	0	?	A	A	A	?	?	P	R	1−3	T 21.2, 20.1
Artistic pillows	2	0	0	A	P	?	?	?	A	?	?	4	
Nest blanket	2	0	0	A	R	H	H	?	?	?	C	1	P 21.3.3
Nest lining	2	0	0	H/C	H/C	H/C	H/C	H/C	H/C	H/C	H/C	1	P 21.3.3
Nest pillow	2	0	0	H/C	H/C	H/C	H/C	H/C	H/C	H/C	H/C	1	P 21.3.3
Nest roof	2	0	0	A	?	H	C	C	C	C	C	1	T 20.1

Notes

Study sites include for Borneo: Gunung Palung (GP), Tanjung Putting (TP), Sabangau (SA) and Tuanan (TU), all *P. p. wurmbii*; and Kutai/Mentoko (KU) and Kinabatangan (KI), both *P. p. morio*; and for Sumatra: Suaq Balimbing (SB) and Ketambe (KE), both *P. abelii*. Prevalence of variants is referred to as: Absent (A), Present (P), Absent for ecological reasons (E), Habitual (H), Customary (C), or not known (?). Contexts are as in van Schaik *et al.* 2006a: subsistence (1), physical comfort (2), and communication (3). "Cultural" refers to the cultural status of the variant as described by Russon *et al*., 2009; Van Schaik *et al*., 2009. The classification of terrestrial versus exclusively arboreal tool variants, extractive-foraging (column name "EF"), and complex tool variants was based on the definitions described in text in the method section. Nest variants are printed in italic and could all be classified as complex, whereas none of the other tool variants could be classified as complex. The "Ref" column mentions the most recent and complete references describing the particular tool variants and their presence data for the eight study populations (1= Wich *et al*., 2009; 2=Shumaker et al., 2011; 3 = Meulman, unpublished data, 4 = van Schaik *et al*., 2003). The "Source" column additionally indicates which tables (T) or paragraphs (P) from Wich *et al.* (2009) were used to retrieve the data. Tool variants for which short names were not reported before, or for which the definition or description has been modified, are: "Bee cover" (cover hat/body with leafy branches or leaves against stinging bees – not swatting), "Branch hide" (combination of "hat hide humans" and "sneaky hat approach"), "Branch reach fruit" (use detached branch to reach incentive), "Branch fan" (fan themselves with branches for cooling); "Club" (tool for hitting a conspecifics with a piece of bark during agonistic interactions); "Aimed missile" (throwing or aimed dropping of branches, large fruits or other objects toward terrestrial predators (or humans), apparently to drive them away); "Stick push spine" (Use a long stick to push a spiny Durian fruit into a crevice and thus protect hands); and "Hat cover" (use of leaves/leafy branches as head cover to protect against rain/strong sun/ etc. – different from "Bee cover" in that usually fewer leaves or branches are used, which are moreover held less closely to the body). Only the variants "Branch dragging display" and "Stick as chisel (1-Nest)" were (sometimes) used in terrestrial contexts.

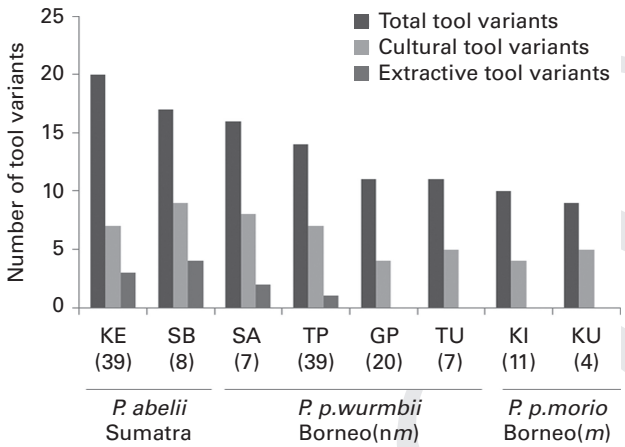

Figure 9.2 Overview of the number of tool variants, cultural tool variants and extractive-foraging tool variants per site. See the legend of Table 9.2 for study site abbreviations. Thirty-eight tool variants were recorded in total over all orangutan populations, of which 16 were cultural and seven were extractive-foraging tools. Both Sumatran populations (KE, SB) are on the higher end of the gradient with respect to the total number of tool variants, the number of cultural tool variants, and the number of extractive-foraging tool variants. In parentheses is the approximate study duration in years for each research site.

reported that study duration did not significantly affect total or cultural (as defined here) tool repertoires.

In contrast to the species-wide total numbers mentioned above, we used *average* numbers per site to compare (sub)species and populations to ensure a fair comparison with the comparative data within orangutans. Figure 9.3 shows the tool repertoire size, and the number of extractive foraging, cultural, complex and terrestrial tool variants (Figure 9.3a), as well as the number of subsistence, physical-comfort and communication tool variants (Figure 9.3b), for orangutans compared with chimpanzees.

Chimpanzees had significantly more complex (MWU = 20; $p = 0.036$), extractive foraging (MWU = 6; $p = 0.001$) and terrestrial (MWU = 0; $p < 0.001$), but not cultural (MWU = 30; $p = 0.390$) tool variants per long-term study site compared with orangutans. The contexts in which tool variants were used also tended to differ between the two species ($\chi^2(2) = 5.58$; $p = 0.061$). Comparing each context separately, we found that chimpanzees had significantly more subsistence tool variants (MWU = 18.5; $p = 0.050$) than orangutans, significantly fewer physical comfort tool variants (MWU = 9; $p = 0.004$), and no substantial differences in the number of communication tool variants (MWU = 38; $p = 0.861$).

Variation in tool-repertoire composition

To establish the main components distinguishing tool repertoires across sites, and to gain some insight into the level of interdependency between outcome variables, we conducted a PCA. The Kaiser–Meyer–Olkin value of the combined set of variables indicated an

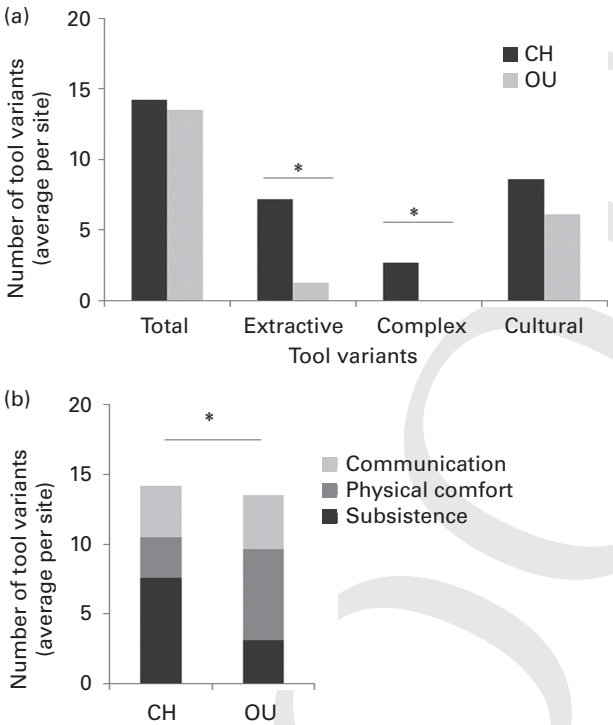

Figure 9.3 The tool repertoires of orangutans and chimpanzees compared. Average numbers for each subset of tool variants are reported to control for the number of study sites and the variation between them. In (a) the average number of tool variants in total, related to extractive foraging, ones that are potentially cultural according to the geographic method, or complex are reported for each of the two great ape species. (b) shows the average distribution of tool variants over the three contexts for the two great ape species. Chimpanzees had significantly more complex (MWU = 20; $p = 0.036$) and extractive-foraging (MWU = 6; $p = 0.001$), but not cultural (MWU = 30; $p = 0.390$) tool variants compared to orangutans. Also, the context in which tool variants were used did tend to differ between the two species ($\chi^2(2) = 5.58$; $p = 0.061$), with chimpanzees having significantly more subsistence tool variants (MWU = 18.5; $p = 0.050$) and significantly fewer physical-comfort tool variants (MWU = 9; $p = 0.004$) relative to orangutans. No substantial differences were found with regard to the number of communication tool variants (MWU = 38; $p = 0.861$).

adequate sampling (when communication variants were excluded – see discussion) for the analysis (KMO = 0.765), although not all KMO values for the individual outcome variables of the tool repertoire were above the acceptance limit of 0.5. Bartlett's test of sphericity ($\chi^2(21) = 177.196$; $p < 0.001$) indicated that correlations between the different outcome variables of the tool repertoire were sufficiently large for a PCA.

Two components had eigenvalues larger than 1 (Kaiser's criterion) and in combination explained 92.9% of the variance (retaining two components was supported by the scree plot). The first component contained the total number of tool variants, the number of extractive foraging, cultural, complex, terrestrial and subsistence tool variants, whereas the second contained the total number of tool variants and physical-comfort tool variants (Table 9.3). In agreement with the predictions based on the refined model, the items that load highly on the

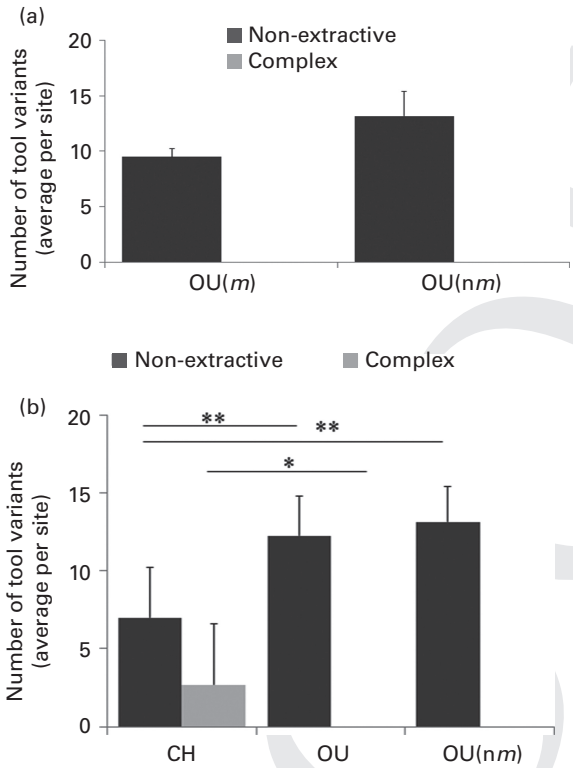

Figure 9.4 The role of intelligence on tool use reflected by the number of non-extractive tools and tool complexity. (a) and (b) show the number of non-extractive tool variants as an indicator of innovative abilities, comparing (a) *P. p. morio* and non-*morio* orangutans ($p = 0.071$) and (b) chimpanzees and non-morio orangutans ($p = 0.001$) or orangutans ($p = 0.002$). The results indicate that *P. p. morio* shows a trend of having less non-extractive tool variants in the repertoire, and that orangutans have significantly more tool innovations in the non-extractive foraging context, compared to chimpanzees. Additionally, complex tool variants are compared between (a) *P. p. morio* and non-*morio* orangutans and (b) non-*morio* orangutans and chimpanzees. The mean number of complex tool variants did not differ significantly between the orangutan populations ($p = 1.000$), but a trend was shown when comparing chimpanzees to non-morio orangutans ($p = 0.093$) or a significant difference between chimpanzees and orangutans ($p = 0.036$); in favor of the chimpanzees).

same components suggest that component 1 represents a general proficiency for the use of foraging tools, whereas component 2 reflects a propensity for using comfort tools.

Testing the four factors of the model

Intelligence and the number of non-extractive and complex tool variants

The first prediction concerning the effect of intelligence was that the repertoire of non-extractive tool variants of Bornean *P. p. morio* is smaller than that of the other orangutans (Table 9.1). We compared the mean number of non-extractive tool variants for the two *P. p. morio* sites with that for all six other orangutan sites (Figure 9.4a). Although, as predicted, *P. p. morio* tended to have fewer non-extractive tool variants than the other orangutans, this

Table 9.3 Results of a principal components analysis (PCA) of tool repertoire outcome variables ($n = 18$ study sites).

Tool repertoire (outcome variables)	Component 1 (Foraging related)		Component 2 (Comfort related)		Component 3 (Communication related)
Rotated factor loadings	−N−C	+N+C	−N−C	+N+C	+N+C
Extractive variants	*0.987*	*0.854*	−0.074	**−0.411**	−0.241
Subsistence variants	*0.968*	*0.925*	0.099	−0.191	0.213
Terrestrial variants	*0.920*	*0.730*	−0.269	**−0.615**	0.194
Cultural variants	*0.893*	*0.900*	0.357	0.115	0.339
Complex variants	*0.885*	*0.952*	0.066	−0.103	0.001
Total # variants	*0.776*	*0.771*	*0.602*	*0.516*	−0.122
Physical-comfort variants	−0.075	0.069	*0.987*	*0.952*	0.206
Nest element variants		−0.234		*0.937*	0.088
Communication variants		0.101		0.157	*0.955*
Eigenvalues	4.946	4.499	1.555	2.681	1.234
Percentage of variance	70.657	49.988	22.215	29.793	13.706

Note
N = nest tool variants, C = communication tool variants, − = excluding, + = including. Positive factor loadings above 0.4 are printed in italic. Negative factor loadings below − 0.4 are printed in bold.

difference was not significant (MWU = 0; $p = 0.071$). We also tested the between-species component of this prediction, namely that non-*morio* orangutans have equal-sized repertoires of non-extractive tool variants as chimpanzees (Figure 9.4b). However, the results show that non-*morio* orangutans have significantly more such tool variants per site than chimpanzees (MWU = 2; $p = 0.001$). Including *P. p. morio* in the analysis did not affect the results (MWU = 7; $p = 0.002$). We will examine this unexpected result in the discussion below.

The second prediction was that tool complexity of *P. p. morio* should be less than that of the other orangutans. Because the orangutan tool repertoire did not include any complex tool variants, it is not surprising that we did not detect any differences in tool complexity between *P. p. morio* and the other orangutans (MWU = 6; $p = 1.000$; Figure 9.4a). The between-species comparison, however, showed that the various chimpanzee populations show a trend of having more complex tool variants than populations of non-*morio* orangutans (Figure 9.4b; MWU = 15; $p = 0.093$). When we included *P. p. morio* in the analysis, this result became significant (MWU = 20; $p = 0.036$). These findings either suggest that innovative ability (as indexed by brain size) does not affect complex tool use, or, more plausibly, reflect the combined effect of tolerant proximity and terrestriality (see below).

Extractive foraging and the number of extractive-foraging tool variants

We predicted more extractive-foraging tool variants for Sumatran versus Bornean orangutans and similar numbers for non-*morio* orangutans and chimpanzees. The number of extractive-foraging tool variants in the local repertoire did not differ significantly (MWU = 0; $p = 0.133$) between non-*morio* Bornean orangutans and the Sumatrans (Figure 9.5a), probably due to the small sample size ($n = 7$). The Sumatra–Borneo difference did become significant when *P. p. morio* were included (MWU = 0;

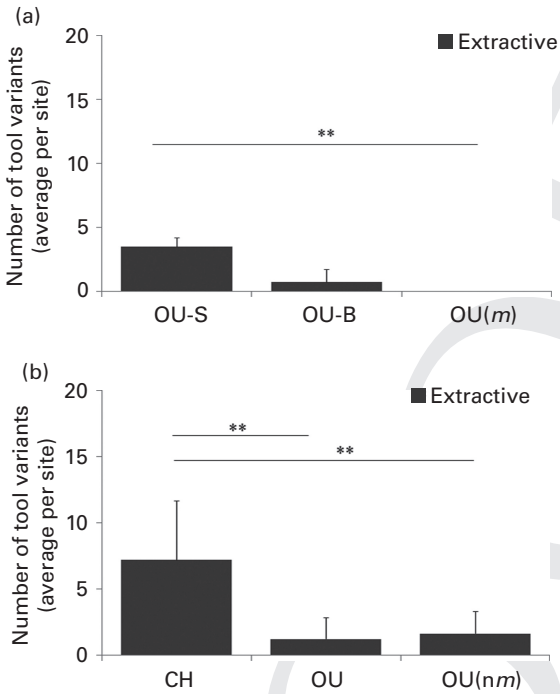

Figure 9.5 The role of extractive foraging on tool use. The number of extractive tool variants are compared between (a) Sumatran orangutans (*P. abelii*) and non-*morio* Bornean orangutans (*P. p. wurmbii*: $p = 0.133$, or $p = 0.036$ when *P. p. morio* were included), and (b) chimpanzees and non-*morio* orangutans (*P. abelii, P. p. wurmbii*; $p = 0.007$) or orangutans (including *P. p. morio*: $p = 0.001$), to evaluate the effect of extractive foraging tendencies. Thus, both Sumatran orangutans and chimpanzees have significantly more extractive foraging tool variants in their repertoire than non-*morio* Bornean orangutans (*P. p. wurmbii*) and non-*morio* orangutans (*P. p. wurmbii* and *P. abelii*), respectively. However, this difference was only significant for the orangutan chimpanzee comparison, probably because of the small number of extractive tool variants within the orangutan tool repertoire (7 out of 38).

$p = 0.036$), suggesting that indeed the abundance of opportunities for extractive foraging may have some effect on the innovation of the relevant tools. However, orangutans have significantly smaller local repertoires of extractive tool variants than chimpanzees (Figure 9.5b; MWU = 6; $p = 0.007$ for non- *morio* orangutans; MWU = 6; $p = 0.001$ for when *P. p. morio* were included). This pattern can be explained by taking the terrestriality effect into account (see below).

Social tolerance and the number of cultural tool variants

The number of cultural tool variants in the local repertoire may be smaller among non-*morio* Bornean orangutans than the Sumatrans (Figure 9.6a), but this difference was not significant (MWU = 1.5; $p = 0.400$ when *P. p. morio* were excluded; $p = 0.143$ when they were included). Similarly, the non-*morio* orangutans do not seem to differ in the number of cultural tool variants from the more gregarious chimpanzees (Figure 9.6b; MWU = 26.5; $p = 0.728$ when *P. p. morio* were excluded; MWU = 30; $p = 0.390$ when they were included). These

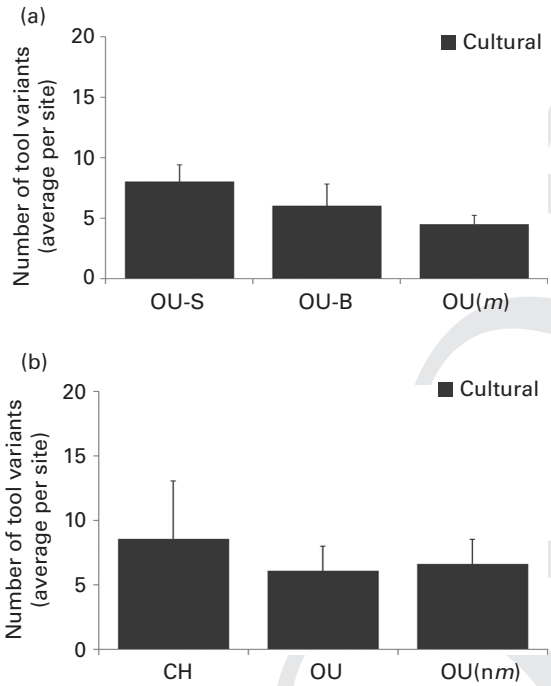

Figure 9.6 The role of social learning opportunities (based on the level of gregariousness), as reflected by the number of cultural tool variants. (a) The non-*morio* Bornean orangutans (*P. p. wurmbii*) have fewer cultural tool variants than the more gregarious Sumatran orangutans (*P. abelii*), although the difference was not significant ($p = 0.400$ when *P. p. morio* were excluded, or $p = 0.143$ when *P. p. morio* were included). (b) The more gregarious chimpanzees also tend to have more cultural variants compared to the less gregarious non-*morio* orangutans ($p = 0.728$) or orangutans ($p = 0.390$), but this difference was again not significant. Hence, social learning opportunities based solely on levels of gregariousness do not explain the variation in the number of tool variants in the cultural tool repertoire.

results, therefore, do not support the contention that increasing opportunities for social learning positively affect the size of the cultural tool repertoire, or at least not to the extent we predicted based on the degree of gregariousness, but do make sense when the effect of terrestriality is included (see below).

The effect of terrestriality

We predicted an effect of terrestriality, especially on the number of extractive (cultural) and complex (cultural) tool variants in favor of the more terrestrial chimpanzees in comparison to the arboreal orangutans (see Table 9.1). Above, we already found that chimpanzees indeed exceed orangutans in the number of extractive and complex tool variants. Likewise, chimpanzees surpassed orangutans in the number of extractive cultural (MWU = 6.5; $p = 0.009$ when *P. p. morio* were excluded; MWU = 7.5; $p = 0.002$ when *P. p. morio* were included) and complex cultural (MWU = 3; $p = 0.002$ when *P. p. morio* were excluded; MWU = 4; $p < 0.001$ when *P. p. morio* were included) tool variants (Figure 9.7). Complex tool variants were, in addition, more often used terrestrially (MWU = 225.5; $p < 0.001$) and extractively

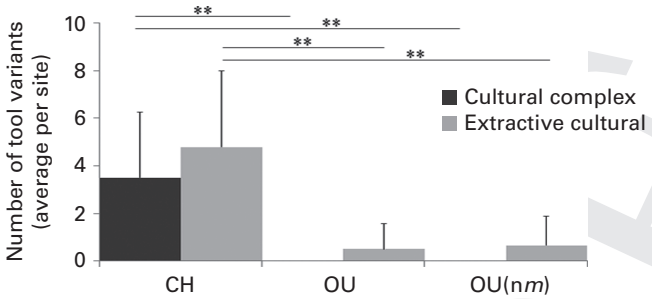

Figure 9.7 Effects of terrestriality on the cultural repertoire of (a) extractive-foraging tools and (b) complex tools; compared between non-*morio* orangutans (*P. abelii*, *P. p. wurmbii*) and chimpanzees. Relative to orangutans, chimpanzees have significantly more cultural tools for extractive foraging ($p = 0.009$ when *P. p. morio* were excluded; or $p = 0.001$ when *P. p. morio* were included) and complex cultural tools ($p = 0.002$ when *P. p. morio* were excluded, or $p = 0.001$ when included).

(MWU = 225.5; $p < 0.001$) than non-complex tool variants. Including terrestriality as a factor thus explains why the effect of intelligence, extractive foraging tendencies and gregariousness *per se*, on the number of complex, extractive and cultural tool variants, is so limited when comparing orangutans and chimpanzees.

Discussion

Support for the refined model

When limiting the comparisons to orangutans only, the results support the original socioecological model (as well as the refined model, because orangutans are rarely terrestrial). First, the various outcome variables of the tool repertoire were always in favor of *P. abelii* and against *P. p. morio*, with *P. p. wurmbii* being intermediate (although mostly non-significant probably due to the small samples of tool variants in a specific category). The exception was tool complexity, because no orangutan population had complex tools. However, flexible and habitual use suggestive of social acquisition have only been reported for seed-extraction and tree-hole tool use, which are both exhibited only by (non-*morio*) Sumatran orangutans (van Schaik *et al*., 1996, 2003b; van Schaik & Knott, 2001).

With regard to the results from the orangutan–chimpanzee comparisons, we found a significant bias toward extractive-foraging, complex, subsistence and terrestrial tool variants in favor of chimpanzees, whereas the bias was in favor of orangutans for the number of non-extractive and physical-comfort tool variants. These results did not support the original socioecological model and underlined the need for invoking a role of terrestriality. This, because the inclusion of terrestriality in the model, improves the fit between (1) opportunities for extractive foraging and the number of extractive tool variants, (2) brain size (as a predictor for intelligence) and the number of complex tool variants, and (3) opportunities for social learning and the cultural tool repertoire. The PCA additionally illustrated a high correlation between terrestrial tool variants into the

first component in which also cultural, complex, extractive-foraging and subsistence tool variants were clustered; in a previous study we furthermore found that, within chimpanzees, terrestrial extractive tool variants are more complex than arboreal tool variants (Meulman *et al*., in press). These results therefore suggest that terrestriality positively affects tool innovations, especially within the extractive foraging context; and, second, that, whereas opportunities for social learning are a necessary precondition for cultural tool variants, terrestriality is additionally needed to increase tool complexity.

Terrestriality versus complex arboreal tool use and nest building

We argue that the terrestriality effect is largely mediated by its effect on opportunities for social learning. A similar effect on tool complexity can therefore be expected for the arboreal honey extraction in chimpanzees when using pounding tools (Meulman *et al*., in press). Likewise, nest building can create a similar effect (again, see Meulman *et al*., in press). Strictly speaking, some variants of orangutan nest building should be regarded as tool use because they involve the detachment of vegetative material(s) from a fixed substrate (see Hansell & Ruxton, 2008 for a more detailed discussion). Interestingly, were we to consider nest-building variants tool use, we would indeed find complex tool use in wild orangutans.

One can also run the same argument in reverse. When a terrestrial context is not associated with enhanced opportunities for social learning, we should not expect to find complex tool use. For instance, male Bornean orangutans are fairly terrestrial but also almost exclusively solitary (apart from brief consortships with females, cf. Utami-Atmoko *et al*., 2009). Indeed, we do not find any complex tool use in male Bornean orangutans.

The importance of species-specific innovation biases

The increased tool complexity in orangutans when including nest variants are in line with the differential challenges faced by orangutans and chimpanzees and the resulting innovation biases of orangutans toward comfort tools and of chimpanzees toward subsistence tools (see also van Schaik *et al*., 2006). These innovation biases also explain the higher number of non-extractive tool variants for orangutans relative to chimpanzees that we could not explain with the model (original or revised).

When we include the five nest elements as tool variants and redo the analyses we indeed find some interesting results. First, the difference between tool complexity in orangutans and chimpanzees, which was significant before, becomes non-significant (MWU = 25, $p = 0.192$ including *P. p. morio*; MWU = 21, $p = 0.357$ excluding *P. p. morio*). In addition, including the five nest elements changed the results of the PCA (KMO = 0.633; Bartlett's test of sphericity: $\chi^2(36) = 205.556$l, $p < 0.001$), so that extractive foraging and terrestrial tool variants loaded strongly negatively on the physical-comfort component, which includes the nest elements (see Table 9.3). Moreover, inclusion of nest elements furthermore changed the percentages of variance explained by the foraging- (50% versus 70% when excluding nests) and comfort-related (30% versus 20% when excluding nests)

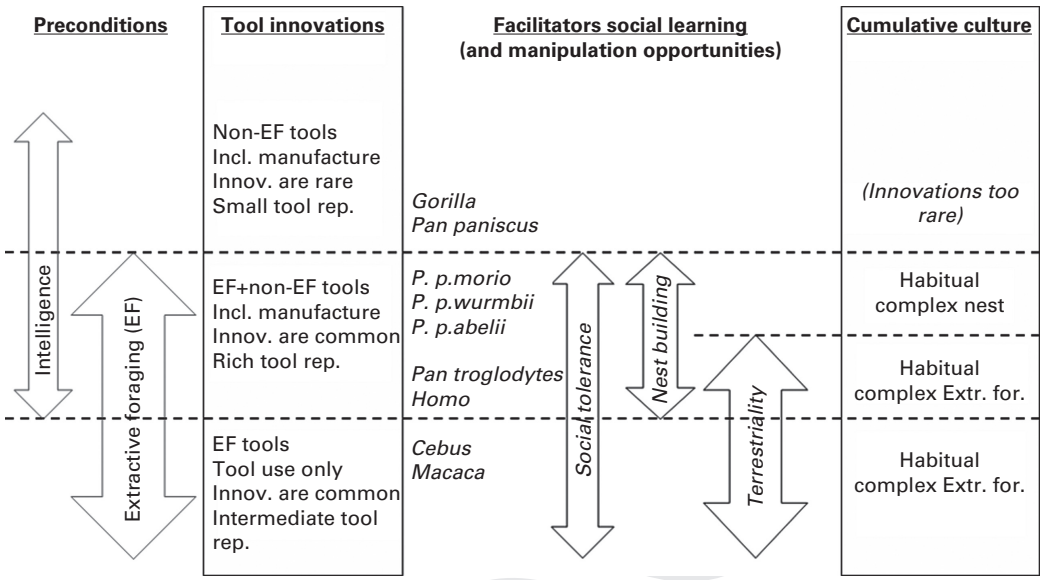

Figure 9.8 Diagram visualizing the five main evolutionary constraints acting on primate tool use. Predictor variables (or evolutionary constraints) are indicated by arrows. The gray rectangles describe the features of the tool repertoires based on these predictor variables. The width of the arrow is associated with its importance for the tool repertoire. The colors indicate the link between the predictor variables and (1) the different features of the tool repertoire, as well as (2) how much they are represented in the different species. The dashed lines designate differences in predictor variables that affect the tool repertoires. Extractive foraging (indicated by EF or Extr. for.) seems to be the main driver for tool innovations (more common and diverse), although intelligence may compensate to some extent by its effect on innovative tendencies (also in the non-extractive-foraging context) and the complexity of these innovations (i.e., manufacture vs. use). Opportunities for social learning subsequently determine whether innovations may persist in the repertoire. Additionally, contexts such as terrestriality and nest building enable more complex manipulations and socially facilitated affordance learning, crucial for the manifestation of cumulative material cultures.

components. Thus, although the foraging-related component still clearly outweighs the comfort-related component, the separation has become less strict. In conclusion, the lower tool complexity in wild orangutans may therefore largely be due to the innovation bias toward arboreal settings and the physical-comfort context.

The evolution of tool use in primates revisited

Based on the variation in orangutan and chimpanzee tool repertoires we can now extrapolate and see what these findings may mean for the evolution of tool use in primates (see Figure 9.8 for a schematic overview). The factors postulated by the original model (extractive foraging, innovative ability [i.e., intelligence] and opportunities for social learning [i.e., social tolerance]) remain relevant, but the effect of intelligence and social tolerance is strongly affected by terrestriality, which therefore must be seen as an essential ingredient of the model.

Extractive foraging remains the basic precondition for tool innovations (Parker & Gibson, 1977; van Schaik *et al*., 1999; Panger, 2007). Apes with extractive foraging have larger tool repertoires than the other apes (bonobos, gorillas) (McGrew *et al*., 2007; Deblauwe & Janssens, 2008; Deblauwe, 2009; Lonsdorf *et al*., 2009; Bentley-Condit & Smith, 2010), and among monkeys the only taxa with habitual tool use comprise extractive foragers that use tools mainly extractively (long-tailed macaques: Gumert *et al*., 2009; capuchins: Visalberghi, 2009). Intelligence may compensate to some extent for the lack of an innovation bias toward the extractive-foraging context, but it has a limited effect on the occurrence of tool innovations in general, and even less on the occurrence of habitual tool use or tools used for extractive foraging. This is reflected in the presence of non-extractive tool variants in all great apes (gorilla and bonobo tool use is almost exclusively non-habitual, non-extractive or even non-foraging related), whereas monkeys have virtually nothing in this regard (Ottoni & Izar, 2008; Gumert *et al*., 2009; Bentley-Condit & Smith, 2010; Shumaker *et al*., 2011).

Opportunities for social transmission determine subsequently whether tool innovations promoted by extractive foraging and intelligence can be maintained in the behavioral repertoire. Although social tolerance explains the presence of habitual tool variants (Whiten *et al*., 2001; van Schaik *et al*., 2003a; Leca *et al*., 2007; Mannu & Ottoni, 2009), it is less important than terrestriality. Terrestriality is important because it facilitates an increased potential for complex innovations and skill acquisition through social learning. Terrestriality (and to a lesser extent also nest building) can therefore additionally explain the "orangutan tool paradox," and the occurrence of habitual and complex tool use in primates in general (for further discussion see Meulman *et al*., in press).

Hominin evolution

The new version of the model (Figure 9.8) can also account for the flourishing of tool use into elaborate lithic technologies during hominin evolution. Since the emergence of the Oldowan, around 2.5 mya, hominins were at least partially terrestrial, and used tools in terrestrial contexts (Plummer, 2004; Foley & Gamble, 2009). In addition, higher sociability (tolerant proximity), as implied by hunting of large game, allowed for more efficient information transfer. The rise of teaching following the adoption of alloparental care (cf. Burkart *et al*., 2009) must have made transfer of technology to subsequent generations more efficient still. Thus, terrestriality, in combination with greater opportunities for social learning, afforded by greater sociability and teaching, goes far to explain the technological differences between great apes and humans (see also Meulman *et al*., in press).

Future directions

Although the new model can encompass the findings of this study, as well as the occurrence of true, habitual and complex tool use in general, the quality of the data could be improved to enable more quantitative analyses. First, more quantitative data on the frequency of extractive foraging (perhaps even classifying whether tool innovations

would be required or not) are important to more quantitatively assess the role of extractive foraging on the evolution of tool use. Second, it may be commendable to distinguish in the future between mere gregariousness and actual opportunities for social learning through observational learning, direct tool transfers and/or indirect tool transfers (or stimulus enhancement). Third, more specific data on variation in the level of terrestriality among populations and its consequences for social proximity and tool affordance learning would be crucial to confirm the importance of terrestriality for the evolution of cumulative technology and cultural intelligence. Especially data on social tolerance levels and socially facilitated skill acquisition in terrestrial contexts versus arboreal contexts would provide us with crucial empirical data in this regard. Likewise, more quantitative data is needed regarding the effect of terrestriality on the occurrence of tool innovations and complex manipulations. Systematic comparisons of complex technology within the nest-building context (when socially learned) could similarly be very interesting and moreover provide more insight on the importance of innovation biases (e.g., chimpanzee versus orangutan nest building). Finally, more species and populations need to be included to confirm our conclusions for primates in general.

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